11. MANIPULATION OF PLANT SPECIES AND COMMUNITIES

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SUMMARY

In an ideal world the design and management of landscape would be founded upon ecological principles. Progress towards this ideal is limited at present by the fragmentary nature of ecological knowledge and ecological research. Some ecologists believe that useful generalizations will be possible only when the results of many more detailed studies are available. This paper explores the alternative view that sufficient pieces of the 'ecological jigsaw' are now available to allow preliminary synthesis and formulation of principles for vegetation management.

INTRODUCTION

The current technologies of landscape construction and maintenance are adaptations of civil engineering, agriculture, horticulture, forestry and gardening and owe little to the science of plant ecology. For historical and practical reasons this is an understandable state of affairs. Until recently the landscape architect has been mainly concerned with the provision and care of mono-specific stands or assemblages of planted species, and in these endeavours he has been well-served by conventional methods of soil preparation, cultivation, weed and pest control.

Over the last decade, three parallel and inter-related changes have occurred which suggest that landscape architecture could now benefit from an infusion of ideas from plant ecology.

1 Expansion of amenity areas, urban and industrial dereliction and motorway construction have created extensive areas of new landscape in need of maintenance or reclamation.

2 Manpower costs have risen to levels which prohibit labour-intensive management except in parkland, gardens and sports-fields.

3 A revolution in agricultural methods and philosophy has resulted in a situation in which farmland (particularly in lowland Britain) can no longer be

relied upon to provide a sanctuary for wildlife and spiritual refreshment for man. A similar change has occurred also in forestry practice.

It has been suggested (Grime 1972; Bradshaw 1977) that an appropriate response to these developments is to indulge in 'creative' ecology and conservation. The objective in this approach to land-use and management is to compensate for shrinkage in the area of attractive countryside by the introduction of more sophisticated techniques which, with low management inputs, will transform 'new' or derelict land into varied, species-rich landscape accessible to the public.

The creation and maintenance of extensive areas of diverse species-rich landscape calls not only for an understanding of the habitat requirements of individual species or populations of plants and animals, but also for sound prediction and control of the species interactions which determine the structure and dynamics of complex, perennial communities over extended periods of time. For such manipulation of processes a greater penetration of ecological concepts into landscape planning and practice seems essential. Here there are communication problems which deserve careful consideration.

COMMUNICATION PROBLEMS

In Fig. 11.1, the communication interface between plant ecologists and those who manage vegetation is represented (a) in an ideal world, (b) as it exists at present and (c) as it might operate in future. Model (b) asserts that whilst the theories and research methods of many ecologists remain strongly influenced by agriculture, forestry and horticulture, efforts to transmit ecological information have encountered strong resistance. This is hardly surprising

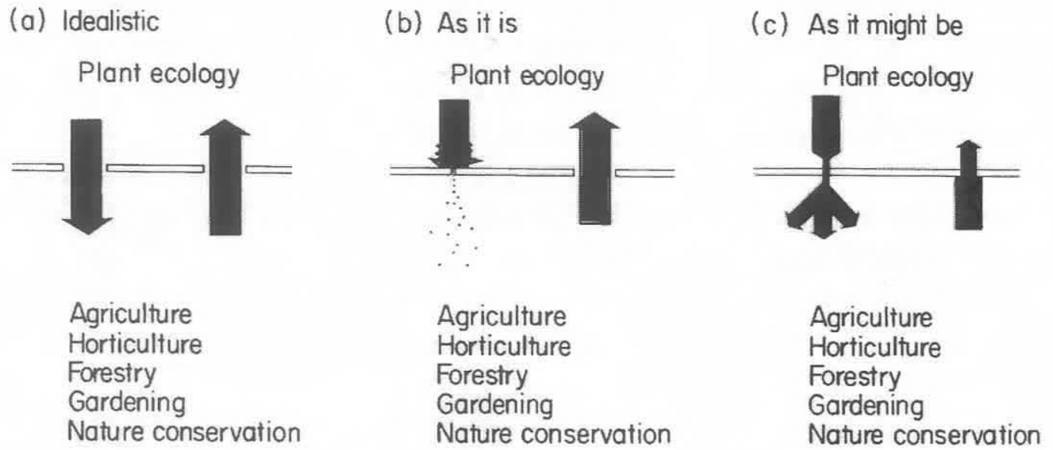

FIG. 11.1. Models representing communication between plant ecologists and those who manage vegetation (a) in an ideal world, (b) as it exists at present and (c) as it might operate in future.

since ecology is a new science and is seeking to influence traditions of land-use which, despite recent transformations, have been established over many centuries. In this situation the main responsibility for the failure in communication must rest with the ecologist. Little is achieved where the information provided by the ecologist is detailed and fragmentary. As suggested in model (c) in Fig. 11.1, greater success is likely where the evidence and ideas are distilled into a broad conceptual framework, the essentials of which are easily communicated by the ecologist and subsequently adapted to particular systems and objectives by those directly engaged in design and management.

Translation of ecological insight and expertise into guidelines for management is hindered further by problems of communication between ecologists. The rapid expansion of ecological research over the last decade has been associated with increasing specialization into schools exploring different approaches such as systems analysis, demography and comparative physiology. Whilst there is no reason to deny the essential contributions of these various fields of activity, it is clear that excessive devotion to particular methodologies (e.g. Gould & Lewontin 1979; Harper 1982; Woolhouse 1981) is limiting communication between specialists and causing delay in the development of ecology as a generalizing and predictive science.

DISTILLATION AND USE OF ECOLOGICAL INFORMATION

During the initial phase of its development, plant ecology has been concerned with the description and classification of vegetation, and much of this research has been conducted by taxonomists who have brought to the subject a characteristic appetite for accuracy and detail. Without denying for a moment the scientific bedrock which this work provides, it would be foolish not to recognize that many of the resulting data are too detailed and specific to be applied directly to management. A similar conclusion must be drawn with respect to the wealth of information which is now becoming available from investigations of the demography, phenology, reproductive biology and physiology of individual species and populations.

It seems imperative, therefore, that means are found by which effectively to distil ecological information into guidelines for vegetation management. As a tentative step towards this objective, the concept of 'plant strategies' has been developed in an attempt to describe, in broad terms, various aspects of the way in which environment and management determine the characteristics of vegetation.

THE CONCEPT OF PLANT STRATEGIES

Before it is possible to predict the consequences of management it is necessary to achieve some general understanding of the processes which cause the structure and species composition of vegetation to vary from place to place and with the passage of time. One approach to this problem is to attempt to recognize the major types of ecological specialization (strategies) which have evolved in plants, and to analyse the role of these strategies in the processes which control the structure, dynamics and species composition of vegetation.

The concept of strategies is of value to vegetation management because it provides a compact framework in which to bring together many disparate threads of ecological information. In particular, it allows a synthesis of data from the work of population biologists and physiological ecologists. Adoption of the term strategy by plant ecologists has attracted some criticism, mainly from 'molecular chauvinists' unwilling to recognize the value of generalizations formulated at the level of the whole plant, rather than its constituent parts. With its teleological implications, the term is not ideal. However, provided that a proper definition is applied, the word can be used with precision. Here a strategy is defined as a grouping of similar or analogous genetic characteristics which recurs widely among species or populations and causes them to show similarities in ecology. Use of the word strategy is also a mark of respect for the pioneer ecologists who first used the term; their achievement was to recognize that organisms do not consist of random assemblages of characteristics but exhibit sets of co-adapted traits which are predictably related to their ecology.

THE THREE PRIMARY PLANT STRATEGIES

In recent years, evidence has been growing that there are, in fact, three primary strategies in plants. Moreover, there is a growing suspicion that analogous strategies occur in algae (Dring 1982), fungi (Pugh 1980; Cooke & Rayner 1984) and animals (Greenslade 1983). This is to suggest that Darwin's 'struggle for existence' can be dissected by recognizing three distinct threats to existence (severe stress, disturbance and competitive exclusion), each occurring under particular types of environmental conditions and each resulting in a different type of evolutionary specialization. The three major threats to plant existence and the strategies which they have evoked will now be described in turn.

Severe stress may be an inherent characteristic of an impoverished environment (e.g. the conditions experienced by lichens on a bare rock), or may be induced or intensified by activities of the vegetation such as dense

shade and sequestration of mineral nutrients in biomass litter or humus (e.g. the conditions experienced by ferns and tree seedlings in a mature beech wood). In contrast with competitive exclusion (see below), we are concerned here with circumstances in which one or more stresses are operating almost continuously throughout the year and constrain the growth of all of the species present in the environment. In consequence, there is little opportunity for the morphology or seasonal pattern of growth of the plant to provide mechanisms of stress avoidance. Under these conditions the successful strategy is that of the *stress-tolerators* which are slow-growing, long-lived evergreens which rely upon the conservative utilization of captured resources and their capacity to survive for long periods during which there may be little growth and reproduction (Fig. 11.2). As a result of their slow growth, stress-tolerators are sensitive to damage; many appear to have evolved highly-effective mechanisms of defence which reduce their palatability to herbivores.

Disturbance is a potent threat to existence in circumstances where there is frequent and severe destruction of the vegetation by herbivores, pathogens or various management procedures (e.g. ploughing, trampling), wind damage, fire or from abrupt changes in climate (frost, drought or flood). Where severe disturbance coincides with continuous stress the habitat is untenable. However, the effect of frequent disturbance in more fertile environments is to promote *ruderals* with rapid growth rates, abbreviated life-spans and prolific reproduction, all of which allow the intervals between disturbances to be effectively exploited (Fig. 11.3).

Competitive exclusion is characteristic of environments which contain an abundance of resources and experience a low intensity of disturbance. Such conditions lead inevitably to occupation by a dense cover of large, rapidly-growing perennial plants capable of high rates of resource capture. This results, over the course of each growing season, in the development of expanding zones of resource depletion above and below the ground surface. In such vegetation, high mortalities occur in those individuals which are outgrown and have their leaves and roots confined to the depleted zones. In these circumstances, the successful strategy is that of the *competitor* which has evolved mechanisms of escape from the depleted zones by constant replacement of the effective leaf and root surfaces during the growing season. In this essentially 'capitalistic' situation, sustained high rates of resource capture and survival depend on high rates of reinvestment of captured resources in the construction of new leaves and roots (Fig. 11.4). A marked contrast may be observed between this system of resource capture and that associated with the stress-tolerator (see above) in which growth is slow and the leaves and roots are relatively immobile, long-lived structures which rely upon resource

FIG. 11.2. A community of 'stress-tolerators' on bare limestone and occupying a shallow crevice of calcareous nutrient-deficient soil: 1, lichens; 2, bryophytes; 3, common rockrose (*Helianthemum nummularium*); 4, meadow oat (*Avenula pratense*); 5, sheep's fescue (*Festuca ovina*).

FIG. 11.3. 'Ruderals' in a frequently disturbed garden plot: 1, groundsel (*Senecio vulgaris*); 2, pearlwort (*Sagina procumbens*); 3, sowthistle (*Sonchus oleraceus*); 4, American willow-herb (*Epilobium adenocaulon*); 5, annual meadow-grass (*Poa annua*); 6, hairy bitter-cress (*Cardamine hirsuta*); 7, large field speedwell (*Veronica persica*).

FIG. 11.4. Two 'competitors' forming a tall dense stand on a stream terrace: 1, reed-grass (*Phalaris arudinacea*); 2, meadow-sweet (*Filipendula ulmaria*).

capture during the brief periods in which there is a relaxation of the severe stresses characteristic of their environments.

The extreme conditions favouring either competitors, stress-tolerators or ruderals form only part of the range of environments exploited by plants. The full spectrum of habitat conditions and associated strategies can be represented in the form of an equilateral triangle (Fig. 11.5) in which the relative importance of competition, stress and disturbance is represented by three sets of contours. This model allows recognition of not only the three extremes of plant specialization described above, but also a range of intermediate strategies associated with less extreme equilibria between stress, disturbance and competition.

A review of the full implications of the model has been presented elsewhere (Grime 1979) and is beyond the scope of this paper. However, reference to the descriptions of the primary strategies (Table 11.1) provides an insight into the wide range of plant characteristics (e.g. life-span, potential growth rate, palatability) which may be expected to change in a predictable manner as we move from one set of environmental conditions to another. The model also

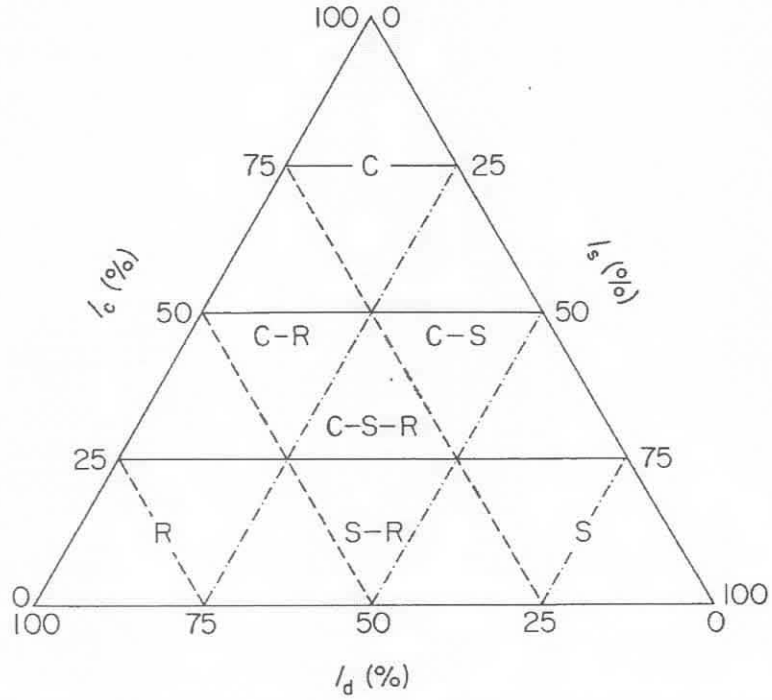

FIG. 11.5. Model describing the various equilibria between competition, stress and disturbance in vegetation and the location of primary and secondary strategies: C, competitor; S, stress-tolerator; R, ruderal; C–R, competitive–ruderal; S–R, stress-tolerant ruderal; C–S, stress-tolerant competitor; C–S–R, 'C–S–R strategist'. I_c, relative importance of competition (——); I_s, relative importance of stress (· — · —); I_d, relative importance of disturbance (— — —).

Table 11.1. Some characteristics of competitive, stress-tolerant and ruderal herbaceous plants

	Competitive	Stress-tolerant	Ruderal
1. Morphology	High dense canopy of leaves. Extensive lateral spread above and below ground	Extremely wide range of growth forms	Small stature, limited lateral spread
2 Leaf form	Robust, often mesomorphic	Often small or leathery, or needle-like	Various, often mesomorphic
3 Canopy structure	Dense rapidly-ascending monolayer	Often multilayered. If monolayer not dense or rapidly-ascending	Various
4 Life-span	Long or relatively short	Long–very long	Very short
5 Longevity of leaves and roots	Relatively short	Long	Short
6 Leaf phenology	Well-defined peaks of leaf production coinciding with periods of maximum potential productivity	Evergreens, with various patterns of leaf production	Short phase of leaf production in period of high potential productivity
7 Phenology of flowering	Flowers produced after (or, more rarely, before) periods of maximum potential productivity	No general relationship between time of flowering and season	Flowers produced early in the life-history
8 Frequency of flowering	Established plants usually flower each year	Intermittent flowering over a long life-history	High frequency of flowering
9 Proportion of annual production devoted to seeds	Small	Small	Large
10 Perennation	Dormant buds and seeds	Stress-tolerant leaves and roots	Dormant seeds
11 Maximum potential relative growth-rate	Rapid	Slow	Rapid
12 Photosynthesis and uptake of mineral nutrients	Strongly seasonal, coinciding with long continuous period of vegetative growth	Opportunistic, often uncoupled from vegetative growth	Opportunistic, coinciding with vegetative growth
13 Storage of photosynthate and mineral nutrients	Most photosynthate and mineral nutrients are rapidly incorporated into vegetative structure but a proportion is stored and forms the capital for expansion of growth in the following growing season	Storage systems in leaves, stems and/or roots	Confined to seeds
14 Defence against herbivory	Often ineffective	Usually effective	Often ineffective
15 Litter decomposition	Rapid	Slow	Rapid

provides a convenient basis on which to predict or explain the changes in species composition which result from alterations of the intensities of stress or disturbance inflicted on the vegetation. These include the changes which follow agricultural dereliction, eutrophication or increases in the frequency of grazing, mowing or trampling. An economic lesson to be drawn from the model is that no vegetation is capable of surviving the combined effect of severe stress and frequent disturbance. This suggests that in attempting to revegetate heavily-trampled but unproductive habitats (e.g. paths which are shaded, on mountains or on maritime cliff-tops), effort has been wasted in pursuit of an unrealistic objective.

USE OF STRATEGY CONCEPTS TO MANIPULATE SPECIES

Despite the growing number of local population studies, it seems inevitable that information relating to *species* will remain as the major currency in communications between ecologists and those engaged in vegetation management. Quite clearly, therefore, it will be helpful to classify species with respect to strategy. It is desirable, however, that any effort to link species with strategies should take account of the capacity of species to expand their ecological range through genetic and phenotypic variation with respect to strategy. By using current knowledge of species and their field distributions it is now possible to begin to estimate the strategic range of common species in Britain. In Fig. 11.6 a triangular ordination of 2008 vegetation samples drawn from all the major habitats of the Sheffield region has been used to examine the ecological amplitude of selected species. The contours in each diagram plot the frequency of occurrence of the species in a matrix of vegetation types, within which each m^2 vegetation sample has been located by reference to selected characteristics (life-history, morphology, phenology, reproduction, etc.) of the component species. A brief account of the ordination procedure and the strategy concepts upon which it is based is provided in Appendix 1. In order to assist interpretation of the contour diagrams, Table 11.1 lists some of the plant characteristics which may be expected to become increasingly prominent in populations, species and vegetation types as we approach the respective corners of the triangle.

When the distributions in Fig. 11.6 are examined, many differences are apparent in terms of both the centre and spread of the contours. The analyses which follow are taken from an earlier attempt (Grime 1984) to interpret the patterns exhibited by the eight species.

Veronica persica: there is a very compact distribution. Restriction to the left-hand corner of the model indicates that this ephemeral species exploits

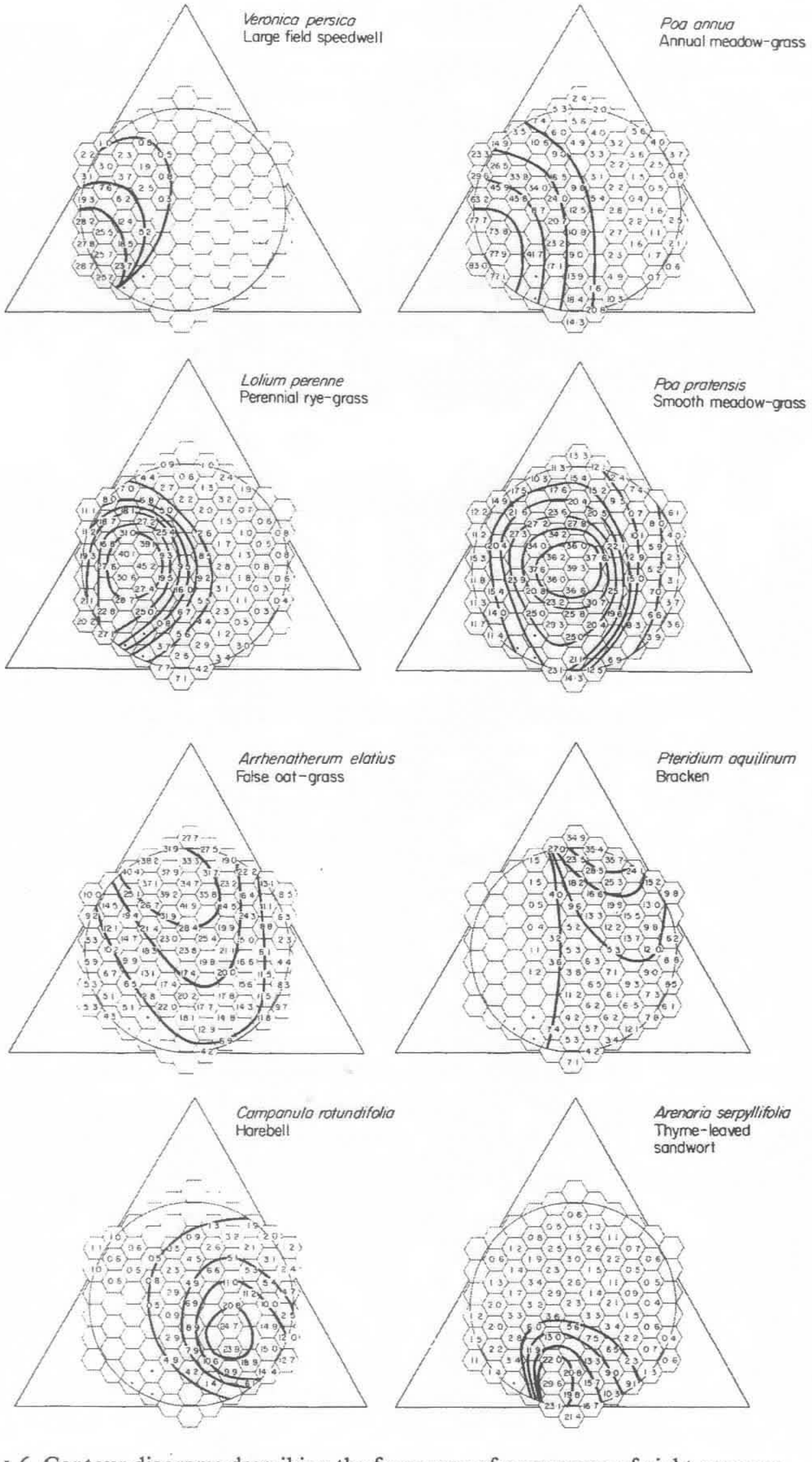

FIG. 11.6. Contour diagrams describing the frequency of occurrence of eight common herbaceous species in a matrix of functionally-defined vegetation types. The procedure used in the triangular ordination is described in Appendix 1. Values indicate the percentage of m² samples containing the species. Contours drawn by eye. *Insufficient data.

productive, heavily-disturbed vegetation, but is unable to colonize infertile habitats and is sensitive to competition from perennial species.

Poa annua: displays a similar concentration in the 'ruderal' corner, but expands into other parts of the model. This distribution is consistent with the results of experimental studies (Law, Bradshaw & Putwain 1977) which show that in addition to the ephemerals of disturbed ground there are perennial genotypes of *Poa annua* which are particularly common in productive pastures.

Lolium perenne: the contours again suggest ruderal characteristics, but they are centred rather higher, indicating sensitivity to heavy disturbance and some ability to persist in perennial communities. The frequency of occurrence of *L. perenne* falls away sharply towards the apex and right-hand side of the triangle, reflecting both the failure of the species to survive in competition with large perennials in productive undisturbed habitats and its exclusion from infertile sites.

Poa pratensis: the distribution is focused in the centre of the triangle, suggesting that the species is particularly associated with vegetation experiencing moderate intensities of stress, disturbance and competition, conditions likely to obtain in the pasture habitats exploited by the species. The contours indicate that, to a remarkable extent, *P. pratensis* is able to extend its range into widely different vegetation types. In our present state of knowledge it is uncertain to what extent this wide amplitude is the result of genotypic variation.

Arrhenatherum elatius: a wide strategic range is also suggested. The highest occurrence coincides with fertile relatively undisturbed conditions (road verges, derelict land, etc.), but the contours also extend towards the base of the triangle, a pattern which may be explained, at least in part, by the occurrence of prostrate genotypes of *A. elatius* shown to be unusually resistant to defoliation (Mahmoud, Grime & Furness 1975).

Pteridium aquilinum: shows a high frequency of occurrence towards the apex of the triangle, a distribution which suggests that the species is a strong competitor with the potential to monopolize plant communities of fertile, relatively-undisturbed sites. The complete absence of the species from the left-hand side of the matrix reflects the failure of *P. aquilinum* to exploit frequently-disturbed habitats. From the descending contours on the right there is evidence of the ability to persist in some unproductive communities such as those associated with heathlands, and heavily-shaded and/or highly acidic woodland herb layers.

Campanula rotundifolia: the contour pattern indicates a well-defined ecology. The species appears to be intolerant of high intensities of disturbance and competition and is restricted to relatively unproductive vegetation.

Arenaria serpyllifolia: concentrated in the area of the triangular model which corresponds to conditions of moderately severe intensities of both stress and disturbance. This accurately portrays the ecology of the species, which is a small winter-annual associated with localities where infertile soils are subjected to disturbance by drought, solifluction or animal activity.

These examples illustrate the potential of strategy concepts to convey in a simple diagram some of the main features of the ecology of a species. It seems reasonable to suggest that information in this form could guide the selection of species for introductions to specific sites and could be used in attempts to manipulate the abundance of particular species. Perhaps most important is the possibility of predicting the fate of species during succession or in response to changes in soil fertility and management regime.

It would be misleading to suggest that all the information required for effective manipulation of a species is contained in the contour diagram. Despite the large number of attributes which vary in association with the axes of the triangular model (Table 11.1), reference to other types of information may be necessary to expose additional species characteristics which are responsible for 'fine-tuning' of their ecology. Data on the frequency of occurrence of species on soils of different pH classes allow predictions of edaphic tolerance and field or laboratory indices of drought and shade tolerance are also desirable. Recently it has been suggested (Grime & Mowforth 1982) that measurements of nuclear DNA content may be used to predict the onset of spring growth, a feature of considerable importance in relation to the timing of cutting, grazing and fertilizer applications.

The most important omissions from the contour diagrams, however, relate to the regenerative biology of the species. In common with other organisms, herbaceous plants may adopt quite different strategies as mature individuals and juveniles, and any summary of the ecology of a species must include consideration of regenerative strategies. Seedlings and vegetative offspring of herbaceous plants are comparatively small and they are exposed to hazards which may be quite different and much more severe than those experienced by established plants. Successful regeneration in many species depends upon exploitation of local and unusually favourable sites, and plants appear to have evolved a variety of regenerative mechanisms which vary in efficiency according to habitat. Five major types of regenerative strategies are distinguished in Table 11.2, which contains also a brief description of the conditions to which each strategy appears to be adapted.

A detailed account of the regenerative strategies and their relevance to management has been provided elsewhere (Grime 1979) and will not be re-stated here. We may conclude, however, that no effort to manipulate a plant species should be attempted without reference to its regenerative biology, a

TABLE 11.2. Five regenerative strategies of widespread occurrence in terrestrial vegetation

Strategy	Habitat conditions to which strategy appears to be adapted
1. Vegetative expansion (V)	Productive or unproductive habitats subject to low intensities of disturbance
2 Seasonal regeneration in vegetation gaps (S)	Habitats subjected to seasonally predictable disturbance by climate or biotic factors
3 Regeneration involving persistent seed or spore bank (B_s)	Habitats subjected to spatially predictable but temporally unpredictable disturbance
4 Regeneration involving numerous widely-dispersed seeds or spores (W)	Habitats relatively inaccessible (cliffs, tree trunks, etc.) or subjected to spatially unpredictable disturbance
5 Regeneration involving persistent juveniles (B_j)	Unproductive habitats subjected to low intensities of disturbance

point already stressed by Grubb (Chapter 6). This is particularly important in projects designed to 'insert' additional species into established vegetation. Failure to provide suitable conditions for establishment is undoubtedly the most common cause of failure in attempts to introduce native species into habitats.

Consideration of regenerative strategies is also highly relevant to efforts to control the abundance of species. In many of the most widely-successful plants (e.g. *Chamaenerion angustifolium*, *Epilobium hirsutum*, *Poa annua*, *Holcus lanatus*) the same genotypes exhibit several regenerative strategies. It seems likely that this versatility explains, at least in part, the ability of these species to invade and persist within a wide range of plant communities. As a corollary, we may suspect that the relative scarcity of certain species, e.g. *Orchis apifera*, *Ophioglossum vulgare*, is related to dependence upon a single regenerative strategy.

MANIPULATION OF PLANT COMMUNITIES

As autecological information accumulates and experience is gained in controlling the distribution and abundance of individual species it seems inevitable that attention will turn to the manipulation of plant communities. Here a particular objective is likely to be the creation of species-rich herbaceous communities, many of which have declined in response to recent changes in land management. Figure 11.7 illustrates a very tentative exploration of the use of strategy concepts to analyse plant communities and devise guidelines for manipulation. Each diagram refers to a m² sample of

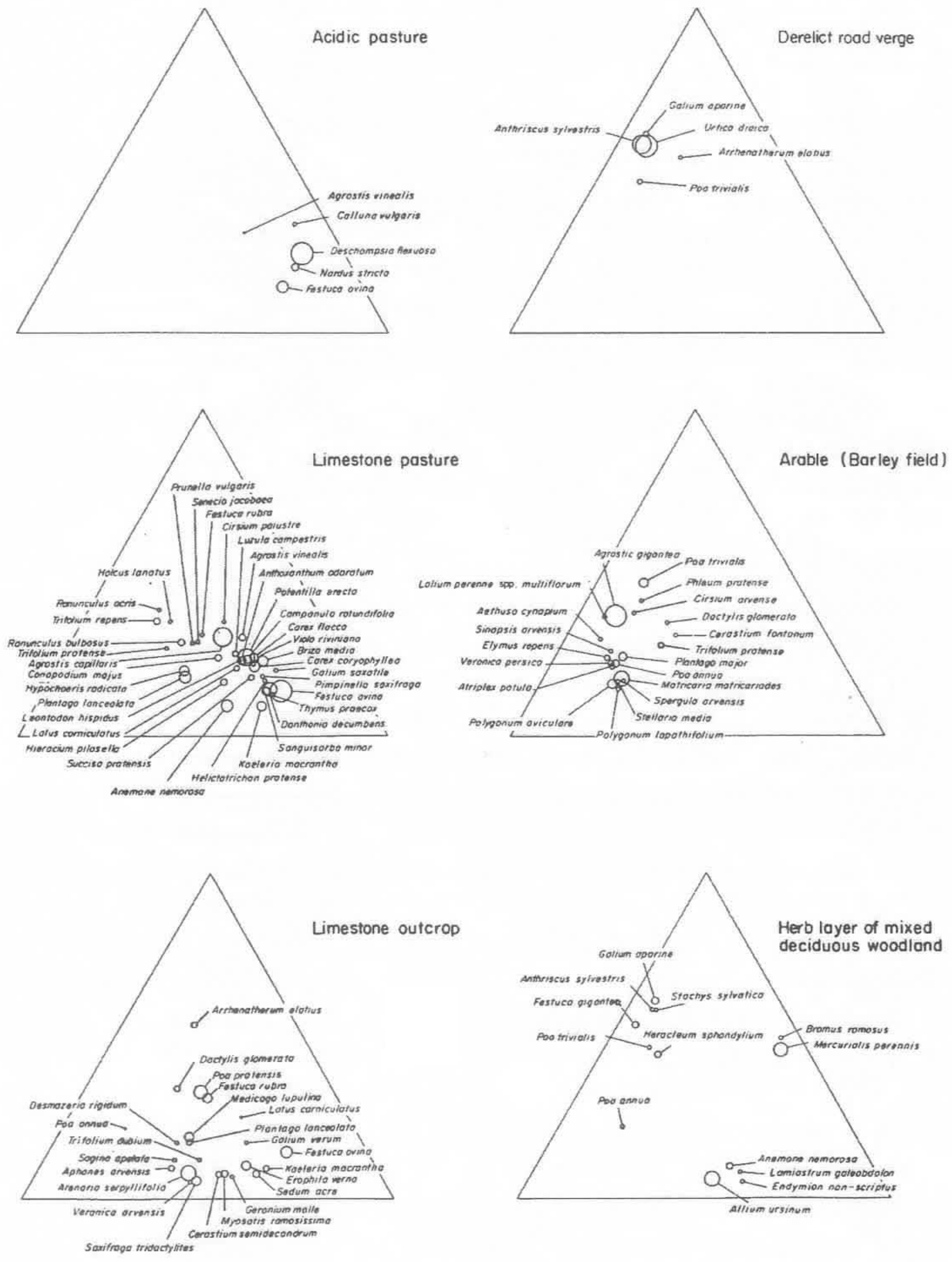

FIG. 11.7. The strategic composition of six contrasted m² samples of vegetation. In each figure the position of each species corresponds to the centre of its contour diagram (see Fig. 11.6) and the size of the circle indicates the abundance of the species within the vegetation.

vegetation for which the abundance of each species is indicated by the size of a circle, the location of which corresponds to the centre of a contour diagram based upon the data and procedure used in Fig. 11.6.

A rather narrow strategic composition is evident in the acidic and calcareous pastures, the arable field and the derelict road verge. A more diverse array of strategies occurs on the limestone outcrop and the woodland herb layer. It may be argued that the range of strategies within these communities has been exaggerated by failure to take account of the particular genotypes and phenotypes represented in each sample. A more likely explanation for the patterns in Fig. 11.7 is that co-existence between different strategies is a widespread phenomenon in plant communities and arises from spatial and temporal variation in the equilibrium between stress, disturbance and competition. In the particular example of the grazed limestone outcrop, spatial niches occupied by contrasted species would be expected to result from effects of variation in soil depth upon mineral nutrient availability and severity of summer drought. Co-existence between plants of very different strategy in the woodland herb layer may be related, at least in part, to temporal niche-differentiation arising from seasonal changes in the quality of growing conditions beneath a deciduous tree canopy.

This first attempt to examine the structure of plant communities by reference to component strategies is both speculative and incomplete; in particular it is necessary to examine also the regenerative strategies which are known to vary considerably within communities (Thompson & Grime 1978). Despite these limitations, however, it is possible to recognize ways in which the diagrams in Fig. 11.7 could be used to initiate or predict changes in the species composition of communities. In the specific case of the grazed limestone outcrop, for example, we may predict that removal of grazing would result in an expansion of the more competitive species *Arrhenatherum elatius*, *Dactylis glomerata* and *Festuca rubra*, and contraction or even loss of many of the small winter annuals situated towards the base of the triangular model. Conversely, an increase in grazing pressure might be expected to shift the balance in favour of the annual species.

Field tests of the usefulness of strategy concepts as a basis for explanation, prediction and control of community processes are now required. Some interesting results are already available from studies in which changes in strategic composition have been recorded in the course of succession (Shepherd 1981), or following changes in management (Buttenschon & Buttenschon 1982), or during fluctuations in climate (Leps *et al.* 1982). There is how an urgent need to set all landscape management on a properly scientific basis; plant strategy concepts will be helpful in this task.

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APPENDIX 1

Brief description of the triangular ordination used in Figs 11.5 and 11.6

The initial step in the ordination was to attempt to classify with respect to strategy the herbaceous species of the Sheffield region. The method involved the use of a dichotomous key (Fig. 11.8) based upon characteristics of life-

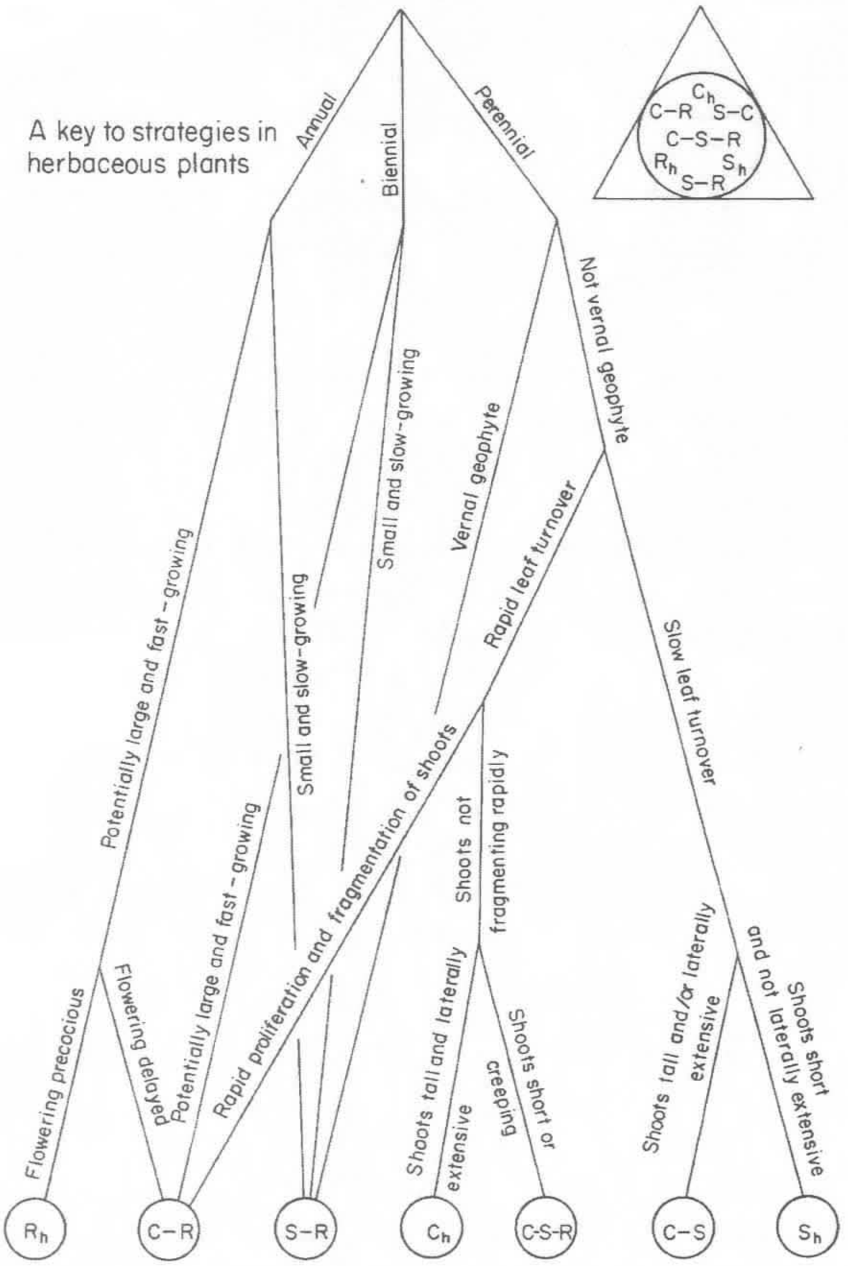

FIG. 11.8. A dichotomous key for the provisional classification of herbaceous plants with respect to strategy. C_h, herbaceous competitor; S_h, herbaceous stress-tolerator; R_h, herbaceous ruderal; C–R, competitive–ruderal; S–R, stress-tolerant ruderal; C–S, stress-tolerant competitor; C–S–R, 'C–S–R strategist'.

history, morphology and phenology and allowed species to be assigned to one of seven positions (Fig. 11.8 inset) corresponding to a characteristic pair of stress and disturbance coordinates and situated within a circular area of the triangular model conforming to the strategic range proposed for herbaceous plants (Grime 1979, Figure 18, page 73). It should be emphasized that this was merely an approximate and provisional classification which could be applied with certainty to only a restricted number of species. No attempt was made to classify species for which critical data were lacking and species known to exhibit major variation in life-history and morphology were also omitted. This procedure allowed the classification of 204 species (henceforward described as marker species) including many of the commoner herbaceous plants of the region.

The next step was to ordinate vegetation samples drawn from the range of habitats represented in the Sheffield region. Each 1-m^2 sample was located in the triangle by reference to the positions and frequencies of the component marker species. This was achieved by calculating mean stress and disturbance coordinates in which the contribution of each marker species was weighted according to its frequency in the vegetation sample. By this procedure, 2008 vegetation samples were ordinated and found to be distributed fairly evenly within the central circular area of the triangle. This allowed a calculation of the percentage occurrence of each species within each of 91 hexagonal zones of the circle and this in turn permitted contours to be drawn describing the distribution of each species.